BIOMETRIC DATA ON THE INFLORESCENCE AND FRUIT OF CRINUM LONGIFOLIUM.

BY J. ARTHUR HARRIS.

I. INTRODUCTORY REMARKS.

Crinum longifolium is familiar to botanists through wide cultivation or through numerous descriptions and figures. At fruiting time, the plants present a remarkable appearance, the massive fruit clusters bending the stalks to the ground, which is strewn with the peculiar seeds. These are exceedingly large and fleshy—fine examples of the bulbiform seeds of the Amaryllidaceae.

Consider some of the problems in the physiology of seed production presented by the inflorescence, fruits and seeds. The form and size of the fruits is closely related to the peculiarities of the seeds. It is neither an elastically dehiscent capsule nor a berry, but resembles a leathern bag, which finally softens to spill out its contents. The number and size of the contained seeds, and consequently the size of the fruit, varies enormously. Some of the seed bags are as large as apples, while others are small sterile knobs terminating the end of the pedicel. In number the seeds range from none to seventy, or more, per fruit; in weight, from nothing to nine grams.

If there are differences in the amount of available plastic material from inflorescence to inflorescence, or from fruit to fruit, or if there is (as has been suggested in biological literature) a competition between the various primordia for the available material, these factors should, it seems to me, be especially easily recognized in structures showing such wide extremes.

These problems attracted my attention several years ago. Partly owing to difficulties inherent in the material, partly

because of the pressure of other work at the fruiting season, I have never been able to complete fully the study as planned in 1905 and 1906. At present, I see no opportunity of returning to it. It seems worth while, therefore, to put on record the data collected and analyzed, together with suggestions toward further work along these lines.

Summarily stated, our problems are:—

(a) To describe certain series of material in terms of biometric constants and their probable errors. These, besides being necessary to the solution of the following problems, may serve as a basis of comparison for fertility characters in other species.

(b) To determine, by comparison with constants for other forms, whether the morphological characters of the reproductive organs in *C. longifolium* can be considered to have any influence upon their variability.

(c) To determine whether the capacity of the inflorescence for maturing its ovaries into fruits is in any degree dependent upon the absolute number of flowers which it produces.

(d) To determine whether the capacity of the ovary for maturing its ovules into seeds is in any degree dependent upon the number of fruits per inflorescence.

(e) To obtain some measure of the differences in the capacity of the inflorescences for maturing ovaries into fruits, ovules into seeds, or for forming large seeds.

II. MATERIAL.

All of the material came from a fine row of *C. longifolium* in the Missouri Botanical Garden[1], which is yearly loaded with the characteristic fruits. In the spring of 1905, I *(a)*

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[1] Dr. Trelease has kindly called my attention to the following point: "The type form is somewhat tinged with red and most of our collection is of this form, but here and there occur white-flowered plants of the var. *album*. I do not believe that you differentiated these when your collections were made and yet I do not believe that they will in any way affect your general results."

counted the number of seeds in a random sample of 1,000 fruits, *(b)* weighed a series of 333 seeds individually, *(c)* determined the number of flowers formed and number of fruits developing as well as the number of seeds per fruit in a series of individual inflorescences.

Collections were again made in 1906. In 309 inflorescences, the number of seeds per fruit was determined in all fruits possible.[2] A lot of 2,000 seeds was weighed.

III. CONSIDERATION OF PROBLEMS.

1. Variation in Number of Flowers and Number of Fruits per Inflorescence.

Data for number of flowers formed and number of fruits developing per inflorescence are given in the totals of the correlation tables for 1905, Table VII, and for 1906, Table VIII. The constants are given in Table I.

TABLE I.

	1905	1906	Difference
Flowers			
Mean	10.668 ± .126	11.518 ± .101	.850 ± .161
S. D.	2.594 ± .089	2.626 ± .071	.032 ± .113
C. V.	24.315 ± .883	22.795 ± .650	1.520 ± 1.096
Fruits			
Mean	5.689 ± .093	7.065 ± .086	1.376 ± .127
S. D.	1.917 ± .066	2.242 ± .061	.325 ± .090
C. V.	33.699 ± 1.282	31.731 ± 1.291	1.968 ± 1.819

[2] It is almost impossible to collect inflorescences at a time to secure the well-developed pods without including some which have lost part of their seeds. There is considerable variation in the time of flowering and a few inflorescences are still in flower when the bulk of the materials must be collected. The later-flowering inflorescences probably produce fewer or smaller fruits, but I have no means of making a quantitative estimate of the difference. The material collected both years was taken almost, if not quite, entirely from the maximum period. Our material is, therefore, to some extent selected. Thus while the statistical investigation of this form is of very great interest, it is surrounded by many difficulties; the results must be interpreted with caution. Some of the difficulties met are discussed in their proper context.

The differences between the two series are of precisely the kind which one would expect from the errors of random sampling, and from slight seasonal influences. The constants are chiefly of importance as a basis for the calculation of correlations. It is interesting, however, to note for comparison with other characters, to be discussed later, that the variability in neither of these cases is at all large. Compare the coefficients of variation with those available for other inflorescences, in Table II. It will be shown that variation in both the number of seeds per fruit and the weight of the seeds is very much higher in *C. longifolium* than in most other species. This is probably referable to the large number of primordia formed and the large size attained by the seeds. Taken together, these render the development of a high proportion of the ovules impossible. Some of the fruits produce a very large number of seeds while others tend to be sterile. Some of the seeds attain a very large size, but the majority must remain small. The immediate interest of these points lies in the fact that no influence of the peculiarities of seed formation upon the type or variability of the parts of the inflorescence can be detected.

TABLE II.

RELATIVE VARIABILITY IN INFLORESCENCES.

Species	Authority and Place of Publication	Coefficient of Variation	
		Flowers	Fruits
Cichorium Intybus.....	De Helguero, Biometrika. **5** : 185.	10.28 — 10.98	......
Staphylea trifolia......	Harris, Biometrika. **6** : 441.	64.44	53.04
Cornus Mas...........	Ritter, Beih. Bot. Centralbl. **25** : 21.	17.83 — 29.72	......
Adoxa Moschatellina...	Harris, Biometrika. **7** : 220.	6.95 — 14.42	......
Nothoscordum striatum	Harris, Rep. Mo. Bot. Gard. **20** : 108.	22.44 — 25.51	......
Allium stellatum.......	" " " " " **20** : 112.	31.79	......
Celastrus scandens	" " " " " **20** : 118.	26.80	48.58
Cercis canadensis.......	Harris, unpublished data.	12.09 — 24.97	......
Sanguisorba officinalis..	Ritter, Beih. Bot. Centralbl. **25** : 7-8.	38.54 — 39.96	......
Anethum graveolens ...	De Vries, The Mut. Theory. **1** : 558-561.	24.07 — 26.50	......
Coriandrum Sativum...	" " " " **1** : 571.	14.37 — 14.48	......

2. The Distribution of Fertility in the Fruits.

The fertility of a fruit is measured by the number of seeds which it produces. Table III gives the number per fruit and the frequencies for:—

(a) A random sample of 1,000 fruits taken in the spring of 1905.

(b) The 768 fruits of the 143 inflorescences with no dehisced fruits collected in the spring of 1905.

(c) The 1,245 fruits comprising the five fertile fruits each from 249 inflorescences of 1906.

(d) The 1,331 fruits from the random selection of eight rays from each of 280 inflorescences in 1906.

TABLE III.

Seeds	a	b	c	d	Seeds	a	b	c	d
1	108	151	57	64	36	10	2	10	16
2	124	104	83	93	37	3	3	11	11
3	108	49	94	100	38	4	2	9	12
4	68	48	74	69	39	2	1	8	5
5	46	40	67	63	40	2	1	6	6
6	34	43	42	43	41	1	2	7	4
7	50	29	45	54	42	2	1	9	5
8	43	29	57	59	43	1	4	9	7
9	36	21	35	46	44	2	.....	6	7
10	26	14	49	48	45	5	2	7	4
11	25	15	31	39	46	.....	.....	2	3
12	37	20	31	35	47	1	1	2	3
13	22	10	26	24	48	1	.....	2	2
14	19	15	28	40	49	.....	.....	3	3
15	20	16	27	25	50	2	.....	4	5
16	26	18	24	23	51	.....	2	2	1
17	12	12	25	30	52	.....	.....	5	3
18	6	8	28	27	53	1	1	1	4
19	12	7	30	26	54	.....	2	2	2
20	16	9	20	27	55	.....	.....	1	1
21	7	13	24	22	56	.....	.....	3	1
22	12	8	22	26	57	1	.....	1	1
23	19	6	23	19	58	.....	.....	1	1
24	8	14	20	27	59	.....	.....	2	.....
25	11	7	12	17	60	.....	.....	.....	1
26	5	9	20	20	61	.....	.....	1	1
27	12	7	20	20	62	.....	.....	.....	.....
28	11	3	17	22	63	.....	.....	1	.....
29	9	4	17	17	64	.....	.....	1	1
30	3	3	12	16	65	.....	.....	1	1
31	4	2	20	15	66	.....	.....	1	1
32	10	3	12	19	67	.....	.....	.....	.....
33	5	1	13	17	68	.....	.....	1	1
34	7	2	9	13	69	.....	.....	.....	.....
35	1	4	11	12	70	.....	.....	1	1

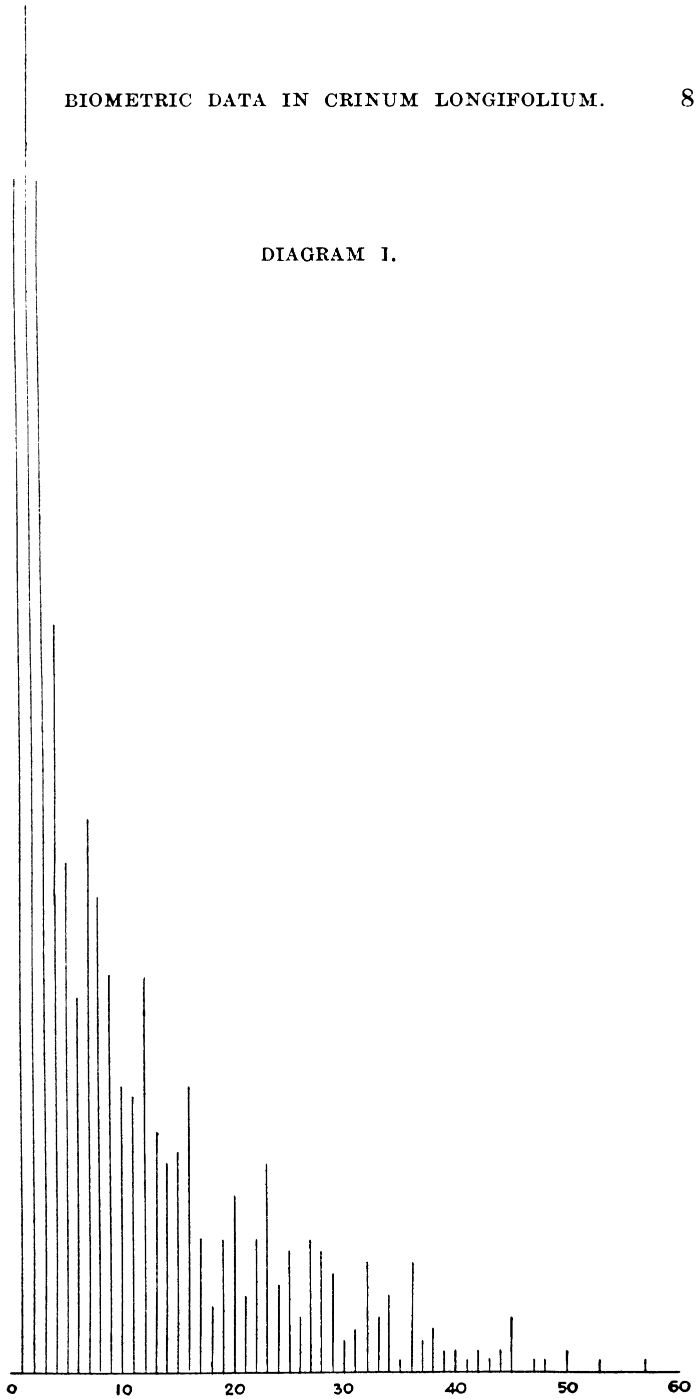
The series *(c)* and *(d)* bear to each other the relation of random sub-samples. Some of the fruits in the two series are identical. The two are inserted merely to show the reader how considerable irregularities may arise through errors of random sampling. Series *(a)* and *(b)* are both samples from the same population, but taken in a somewhat different manner. Diagram 1, in which the heights of the several vertical lines represent the frequencies for the 57 classes of fruits, gives the 1905 random sample. The statistical constants are given in Table IV.

TABLE IV.

Series	Mean Seeds	Standard Deviation	Coefficient of Variation
(a) 1905..........	10.338 ± .221	10.342 ± .156	99.55
(b) 1905..........	9.242 ± .246	10.095 ± .174	109.23
(c) 1906..........	15.471 ± .225	13.344 ± .180	86.25
(d) 1906..........	15.283 ± .239	12.941 ± .169	84.67

Two characteristics of these distributions are remarkable. The range of variation is exceedingly wide. The mode lies far to the lower end of the range, the most frequent cases being fruits with but a single seed or, at most, three seeds.

DIAGRAM I.



The frequencies of various numbers of seeds per fruit are represented by the heights of the ordinates.

A comparison of the frequencies in Table III reveals dissimilarities too great to be attributed solely to the probable errors of random sampling.[3] Even the two samples of 1905 seem to differ far more, in the frequencies of the first three classes at least, than can be explained by the errors of sampling from a homogeneous population. Series *(a)* seems to have a significantly higher mean than series *(b)*. The difference is over thrice its probable error and confirms the impressions from the frequency distributions. Probably the difference in the method of collection of these two lots of material introduced some unknown biological factor to which the differentiation is due.[4] In the 1906 series, the empirical mode is on 3 instead of 1 or 2. The mean and standard deviations are also higher and the range is wider than in the 1905 collections.

The coefficients of variation show how exceedingly great the variability in this material really is. The reader will appreciate this by a comparison of the constants for several other species of plants, as given in Table V.

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[3] How great such differences may be for individual classes may be seen by a comparison of the frequencies in series *(c)* and *(d)*. Naturally, the reader will remember that these are actual, not relative, frequencies, and that in one case, $N = 1245$, while in the other, $N = 1331$.

[4] The difficulties of collecting really typical samples of material (already discussed in an earlier section), while at the same time retaining data for all the characteristics which it was desired to consider, was one of the chief reasons for discontinuing the study of *Crinum*.

TABLE V.

VARIABILITY IN NUMBER OF OVULES AND NUMBER OF SEEDS PER LOCULE (l) AND PER FRUIT (f).

Species	Authority and Place of Publication	Ovules per Fruit	Seeds per Fruit
Sanguinaria canadensis	Harris, Biometrika. **7** : 309-310.	30.28 — 30.66	32.66 — 39.26
Robina Pseud-acacia...	" " **6** : 442.	18.69	45.45
Hibiscus militaris (l)...	" " **8** : 55-64.	....	20.70
" lasiocarpos (l)	" " **8** : 55-64.	....	32.88
" Moscheutos (l)	" " **8** : 55-64.	....	18.93
" Trionum (l)..	" " **8** : 55-64.	17.49	22.58
" syriacus (f) ..	" " **8** : 55-64.	8.79 — 10.21	27.65 — 46.78
" " (l) ..	" " **8** : 55-64.	11.15 — 13.80	34.91 — 54.35
" Manihot (l) ..	" " **8** : 55-64.	13.27	35.55
Celastrus scandens	Harris, Rep. M. B. G. **20** : 122.	....	31.42
Cytisus scoparius......	Harris, Amer. Nat. **43** : 354.	....	35.24
" "	Pearson, Phil. Trans. A. **197** : 335.	....	36.78
Cercis canadensis......	Harris, Bot. Gaz. **50** : 121.	19.26	26.71
Nelumbium luteum....	Pearl, Amer. Nat. **40** : 760.	....	17.45
Lotus corniculatus....	Pearson, Phil. Trans. A. **197** : 367.	....	46.38 — 52.14
Lathyrus odoratus.....	" " " " **197** : 367.	12.65 — 13.39	27.67 — 34.96
" sylvestris....	" " " " **197** : 367.	6.79	32.91
Vicia Faba...........	" " " " **197** : 367.	....	33.50
Vicia hirsuta..........	" " " " **197** : 367.	30.88	38.32

In percentage variability of number of seeds per fruit, *Crinum* stands far above any of the considerable number of species given in this table. Only in *Staphylea trifolia*[5] have I found coefficients of variation at all comparable in magnitude. These two species agree in having very skew distributions of number of seeds per fruit, but differ widely in range and mean, the mean number of seeds per fruit in *Crinum* falling in the neighborhood of the maximum number in *Staphylea.* When a sufficiently wide series of these exceptional cases are gotten together, discussions of the underlying morphological and physiological factors to which their peculiarities are due can be profitably undertaken.

3. Variation in Seed Weight.

An investigation of the size of the exceedingly variable seeds of this form presents two serious difficulties. They are so irregular that weighing is the only feasible method

[5] For the data on which these statements are made see four papers: Biometrika **7** : 453–504. 1910. — Zeitschr. f. Ind. Abs.-u. Vererbungsl. **5** : 173–188. 1911.—Beih. Bot. Centralbl. **28** : 1–16. 1912. —Bot. Gaz. **53** : 204–218; 396–414. 1912.

of measurement. Only fully matured seeds should be weighed, but one fruit of an inflorescence may be quite mature, while others are apparently still in a developing condition.

The first difficulty demands only time and patience. The second may be fairly well met by choosing only fruits with well-ripened walls, though even here some of the smaller seeds seem immature.

In 1905, 333 seeds, taken quite at random, were weighed and seriated in units of half a gram range. The method of collection of another sample of 2,000 in 1906 is described under Section 7. Table VI gives the data.

TABLE VI.

Class	1905	1906	Class	1905	1906
1 = 0 — 0.50	22	219	10 = 4.51 — 5.00	10	39
2 = 0.51 — 1.00	31	396	11 = 5.01 — 5.50	5	27
3 = 1.01 — 1.50	57	352	12 = 5.51 — 6.00	6	26
4 = 1.51 — 2.00	33	290	13 = 6.01 — 6.50	6	29
5 = 2.01 — 2.50	45	212	14 = 6.51 — 7.00	5	13
6 = 2.51 — 3.00	40	147	15 = 7.01 — 7.50	2	5
7 = 3.01 — 3.50	20	106	16 = 7.51 — 8.00	1	6
8 = 3.51 — 4.00	26	76	17 = 8.01 — 8.50	2	1
9 = 4.01 — 4.50	22	55	18 = 8.51 — 9.00	....	1

The distribution of weight of seed, like that of the number of seeds per fruit, cannot by any stretch of the imagination be regarded as conforming to the "normal," Gaussian, or "Quetelet's" curve, which some biologists seem to regard as the biologically normal type. The skewness is very conspicuous. The great majority of the seeds remain very small—those attaining a large size are rare. To what extent this may be due to a competition of the numerous ovules for a supply of food material, which is inadequate to bring many seeds up to the large size which we think of as characteristic of the bulbiform seeds of the Amaryllidaceae, can only be determined by further investigation along lines indicated later.

For constants (in the half gram units as indicated in the tables) I find:

Mean Weight of Seed:—

1905	5.565 ± .121
1906	4.369 ± .045
Diff.	1.176 ± .129

Standard Deviation:—

1905	3.282 ± .086
1906	2.971 ± .032
Diff.	.311 ± .092

Coefficient of Variation:—

1905	58.972 ± 2.007
1906	67.697 ± 1.000
Diff.	8.725 ± 2.242

Apparently, the two series differ significantly in mean weight of seed, those for 1905 being about half a gram heavier than those of 1906. This is not at all a surprising result, for the weight of a *Crinum* seed must depend, in large measure, upon availability of plastic material and water. The variability, as shown by the coefficient of variation, is very great. Perhaps the variability differs for the two years, but because of the skewness of distribution, the probable errors calculated by the ordinary formulæ may not give decisive tests.

The relative variabilities for seed weight, like those for number of seeds per pod, are high, but data for comparison from other species are rare. Johannsen[6] gives coefficients of variation of from 10.5 to 17.5 for "pure lines" of beans, and I have found generally comparable values for large series of *Phaseolus vulgaris*. I know of no other data.

4. The Relationship between the Size of the Inflorescence and its Capacity for maturing Fruits.

This problem has already been considered for immature

[6] Rep. Third Int. Conf. Genetics 109. 1907.

inflorescences of *Staphylea*[7] and for mature inflorescences of *Celastrus*.[8] The correlation between the number of rays per inflorescence and the number bearing a fertile fruit appears in the 1905 series, in Table VII, and for the 1906 series in Table VIII.

TABLE VII.

Fruits Matured.

		2	3	4	5	6	7	8	9	10	11	12	
Flowers Formed.	6	....	3	3	3	....	....	....	....	....	....	....	9
	7	....	2	2	4	1	1	....	....	....	....	....	10
	8	2	4	8	4	6	2	1	....	....	....	....	27
	9	....	4	3	2	8	6	1	....	....	....	....	24
	10	....	2	3	8	6	4	5	1	....	....	....	29
	11	1	3	4	3	5	1	3	....	1	1	....	22
	12	....	1	6	2	3	3	5	1	....	....	....	21
	13	....	....	3	1	3	3	3	3	....	....	....	16
	14	....	3	4	4	3	2	4	1	....	....	1	22
	15	....	....	....	....	2	2	1	....	2	....	....	7
	16	....	....	....	....	1	3	....	....	....	....	....	4
	17	....	....	....	....	....	....	....	1	1	....	....	2
		3	22	36	31	38	27	23	7	4	1	1	193

TABLE VIII.

Fruits Matured.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14	
Flowers Formed.	4	...	...	...	1	...	...	...	...	...	...	...	...	...	...	1
	7	...	...	1	1	2	2	1	...	...	...	...	...	...	...	7
	8	...	...	...	4	11	11	8	1	...	...	...	...	...	...	35
	9	...	...	1	3	4	6	10	3	1	...	...	...	...	...	28
	10	...	1	1	2	6	11	12	6	4	3	...	...	...	...	46
	11	1	...	2	...	8	7	3	5	5	4	1	...	...	...	36
	12	...	...	...	4	5	6	8	4	6	5	4	2	...	...	44
	13	1	...	...	1	4	6	5	6	5	8	4	2	1	...	43
	14	...	1	...	5	2	3	5	3	7	4	2	3	...	1	36
	15	...	...	1	2	3	...	2	2	2	1	1	1	...	...	15
	16	...	...	...	...	1	3	1	1	2	1	...	...	...	...	9
	17	...	...	...	...	...	...	2	2	...	...	...	...	...	...	4
	18	...	...	...	...	...	1	1	...	2	1	...	...	...	...	5
		2	2	6	23	46	56	58	33	34	27	12	8	1	1	309

7 Harris, J. Arthur. Biometrika **6** : 439–441. 1909.
8 Harris, J. Arthur. Ann. Rept. Mo. Bot. Gard. **20** : 117–119. 1909.

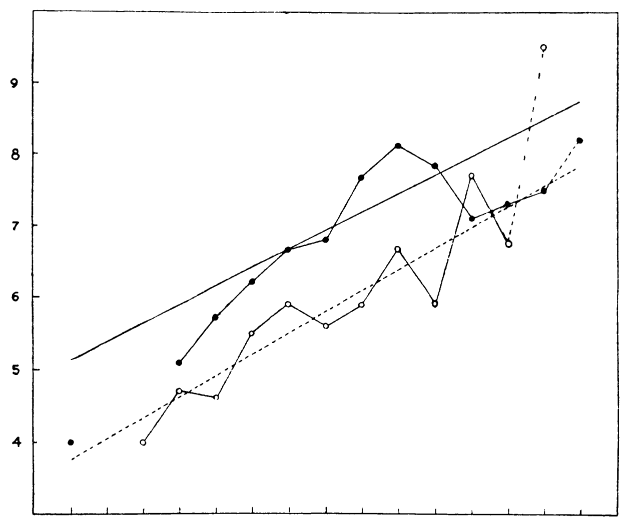
That the inflorescences with a number of flowers above the average produce more than the average number of fruits is clear from mere inspection of the tables. That the relationship is not a very close one is shown by the correlation coefficients for number of flowers and number of fruits which are:—

$$\text{For 1905, } r_{ff} = .393 \pm .041$$
$$\text{For 1906, } r_{ff} = .305 \pm .035$$
$$\text{Difference} = .088 \pm .054$$

Considering the smallness of the samples, the agreement is good.

The relationship between the two characters is shown graphically in Diagram 2, where the two lines are given by the straight line regression equations:—

DIAGRAM II.
REGRESSION OF NUMBER OF FRUITS MATURING ON NUMBER OF FLOWERS FORMED.



1905 series, circles and broken line; 1906 series, solid dots and firm line.

$$\text{For 1905, } fr = 2.5912 + .2904\ fl.$$
$$\text{For 1906, } fr = 4.0703 + .2600\ fl.$$

The lines are apparently a fairly good smoothing of the

empirical means—considering the smallness of the available samples. The means for 1906 perhaps suggest nonlinear regression, but our data hardly justify further statistical treatment. The coefficient of correlation, *r,* may without further test be regarded as a *fairly* satisfactory measure of the relationship under consideration.

Here, as in the inflorescences already studied, we cannot be satisfied with the information given by the coefficient of correlation for number of flowers and number of fruits per inflorescence. The clusters with the larger number of flowers would be expected to produce more than the average number of fruits, providing that the chances of an individual flowers producing a fruit is not, in some measure, dependent upon the number of flowers in the inflorescence upon which it is borne.

The constant which we desire is r_{xz}, where x is to be read as number of flowers per inflorescence and z as the deviation of the number of fruits per inflorescence from their probable value, on the assumption that the chances of a flower producing a fruit is independent of the number of flowers per inflorescence.

Using the formula

$$r_{xz} = \frac{r_{xy} - V_x / V_y}{\sqrt{1 - r_{xy}^2 + (r_{xy} - V_x / V_y)^2}}$$

where x denotes number of flowers and y number of fruits, I find:—

For 1905, $r_{xz} = -.337 \pm .043$
For 1906, $r_{xz} = -.399 \pm .032$
Difference $= .062 \pm .053$

Again the agreement of the two series is as close as one could expect, having regard to the probable errors. The signs show that as the number of rays per inflorescence increases, the capacity of the individual rays for maturing their ovules into seeds decreases, and to a considerable extent.

The other two cases, which have been investigated give:—

$$\text{For } Staphylea,\ r_{xz} = -.649 \pm .024$$
$$\text{For } Celastrus,\ r_{xz} = +.024 \pm .034$$

The *Staphylea* material was a lot of immature inflorescences in which further failures would have taken place before maturity. The *Celastrus* series shows that the results obtained for *Crinum* cannot be regarded as general. Only the investigation of many further series of data will enable one to speak with confidence concerning the relationship of the size of the inflorescence to its capacity for maturing its ovaries into fruits, or to discuss the factors involved. The constants already calculated suggest that the problem is one of real physiological interest.

5. The Relationship between the Number of Fruits per Inflorescence and the Number of Seeds produced.

A first step in ascertaining the factors which are active in determining the fertility of a fruit may be taken in the calculation of the correlation between the number of fruits per inflorescence and the number of seeds which these fruits contain.[9] If the development of an abnormally large number of fruits per inflorescence makes severe demands upon the plastic materials which can be supplied to it, then, one might expect a negative correlation between the number of fruits matured and the number of seeds developing per fruit. On the other hand, the greater number of fruits on some inflorescences may merely indicate superior vigor, or feeding; in this case, the number of seeds per fruit might tend to increase as the number of fruits per inflorescence becomes larger. Doubtless both are active factors and must ultimately be analyzed out and measured individually. Doubtless the two factors tend, in many cases, to cancel each other, giving a resultant correla-

[9] This has been done for an extensive series of fruits of *Staphylea*. See two papers, one in the Botanical Gazette **53**: 204–218; 396–414. 1912; and another in the Beihefte zum Botanischen Centralblatt I. **28**: 1–16. 1912.

tion of *circa* 0. Preliminarily, I have thought it worth while to determine in a few cases what the actual correlations are. Such results must be of service in planning more detailed and critical studies.

Unfortunately, only the small series of inflorescences for 1905 is available for our present purposes.[10] The correlation between number of fruits per inflorescence and number of seeds per fruit (fruits per inflorescence weighted with the number of seeds which they produce) is shown with a 5-unit grouping for the seeds in Table IX.[11] The constant is

$$r = -.072 \pm .024$$ [12]

TABLE IX.

SEEDS PER FRUIT.

Fruits per Inflorescence	1-5	6-10	11-15	16-20	21-25	26-30	31-35	36-40	41-45	46-50	51-55	
2	1	....	....	1	2	....	1	....	....	....	1	6
3	24	11	8	7	6	6	2	1	1	....	....	66
4	64	22	8	14	11	2	3	1	2	1	....	128
5	68	18	7	6	6	2	1	2	....	....	....	110
6	65	26	16	7	12	6	2	2	1	....	1	138
7	76	23	16	11	5	....	1	....	1	....	....	133
8	64	17	12	6	5	8	2	2	2	....	2	120
9	13	11	7	1	....	2	....	1	1	....	....	36
10	9	6	1	1	1	....	....	....	1	....	1	20
11	8	2	1	....	....	....	....	....	....	....	....	11
	392	136	76	54	48	26	12	9	9	1	5	768

Apparently, therefore, the production of a number of fruits

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10 These were only 193 in number and 50 had one or more of the fruits dehisced, so that the number of seeds in them could not be obtained. These fruits probably represent, on the average, those containing the greatest number of seeds, since these ripen first. It seemed best, therefore, to discard all inflorescences in which dehisced fruits were found.

11 Probably grouping by fives is too coarse, where variation is as skew as it is here. In another study this point should be regarded.

12 This was obtained by using 768, the number of fruits, as N. If the number of inflorescences, $N = 143$, be used, we have $r = -.072 \pm .056$

above the average tends to cut down the number of seeds in these fruits,[13] but much confirmatory evidence must be obtained before great stress can be laid on such a weak correlation.

The only directly comparable series are one for *Celastrus*[14] and several for *Staphylea*.[15] For *Celastrus* there is no trustworthy indication of an interdependence between the number of flowers formed per inflorescence and the number of seeds maturing per fruit, or between the number of fruits matured per inflorescence and the number of seeds matured per fruit.

For *Staphylea* the results show the most slender relationships between numbers of fruits per inflorescence and the fertility of the fruits. Data for both ovules and seeds are available. For twenty individual shrubs of 1906, the mean relationship for number of fruits per inflorescence and number of ovules per locule is only $r = +.0192 \pm .0185$ —a value of no significance. For fruits and seeds it is $r = -.0399 \pm .0080$, indicating that in *Staphylea* the condition may be similar to that in *Crinum*. For the whole populations the results are:—

	For Ovules.	For Seeds.
1906,	$r = +.0391 \pm .0086$	$r = -.0474 \pm .0086$
1908,	$r = +.0633 \pm .0061$	$r = -.0494 \pm .0061$
1909,	$r = -.0539 \pm .0085$	$r = +.0626 \pm .0085$

Taken as a whole, the data for *Staphylea* indicate a very slight negative correlation between the number of fruits matured and the capacity of these fruits for developing their ovules into seeds.

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13 Waldron (Am. Nat. **44** : 48–56. 1910.) concludes that the seeds are lighter in large heads of oats than in small ones. Harris (Torreya **11** : 165–169. 1911.) has shown that in *Staphylea* and *Cladrastis*, the weight of the seed is in some measure dependent upon the number produced in the fruit. As noted above, other data are in press, and still more are being reduced.

14 Harris, J. Arthur. Ann. Rept. Mo. Bot. Gard. **20** : 116–122. 1909.

15 Harris, J. Arthur. Beih. Bot. Centralbl. I. **28** : 2–10. 1912.

But altogether the evidence confirms the conclusions from another study[16] that the correlation between somatic characters and fertility is generally very slight.

6. Correlation in Seed Production between the Fruits of the Inflorescence.

If the number of seeds which develop per fruit is dependent upon the available plastic material, as seems somewhat probable from the results of the two preceding sections, then one might expect an intra-inflorescence correlation for number of seeds per fruit. That is, one would expect that the characters of an individual fruit—judged in comparison with the condition in the population as a whole as a standard—would not be independent of, but correlated with, those of the other fruits of the inflorescence.

The great difficulty of the problem lies in its complexity. Within a given inflorescence an abnormally large number of seeds in one fruit might necessitate an abnormally small number in another fruit, because of the inadequacy of plastic materials. But the available materials may differ widely from inflorescence to inflorescence, and as a consequence, all of the fruits of some inflorescences be much better supplied than those of others. The tendency of the first of these putative conditions would be to produce a negative correlation between the number of seeds per fruit of the inflorescence, while that of the second would be to bring about a positive correlation. As yet, I see no way of differentiating these factors and estimating their relative intensities. Certainly, this is not possible in the present material. It seems worth while, however, to make a beginning in the problem by determining what the actually existing correlation is.[17]

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16 Harris, J. Arthur. On the Correlation between Somatic Characters and Fertility. Biometrika **8** : 52–65. 1911.

17 This problem is being considered in some detail for a widely different species. See a paper, The Influence of the Seed upon the Size of the Fruit in *Staphylea,* in the Botanical Gazette **53** : 204–218; 396–414. 1912.

From the material collected in the spring of 1906, it is possible to form correlation tables for the number of seeds per fruit in the same inflorescence.

A difficulty at once arises in regard to the selection of fruits to represent the inflorescences. The complete failure of some flowers to produce seeds may, perhaps, affect the number which develop in other ovaries of that inflorescence. It is difficult to decide in advance whether all pedicels shall be chosen quite at random and the sterile ones inserted in the series, or whether all pedicels bearing no fruits shall be excluded.

From the 1906 lot of material, it is possible to extract two series. The first comprises 249 inflorescences bearing five fruits each. It would have been slightly better, perhaps, if all the fruits from these inflorescences had been used, but the labor of dealing with the correlations is excessive. The second series comprises 280 inflorescences each yielding eight pedicels with or without fruits.[18] In both of these series the pedicels or fruits were chosen quite at chance by a system of numbering the recorded data backwards and forwards.

The tabling of the data presented a problem of the greatest difficulty. As compared with many symmetrical intra-class correlation surfaces which have been formed, the number of entries is small, being only $5 \times 4 \times 249 = 4{,}980$ for the table containing fertile fruits only and $8 \times 7 \times 280 = 15{,}680$ for the surface comprising both sterile and fertile rays. But the range of variation in number of seeds is so great—from 0 to 70—that the tables are exceedingly large, comprising 4,900 and 5,041 compartments respectively. It is not safe to reduce the surface of the table by grouping, because of the skewness of distribution.

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[18] Sterile fruits were counted in with those in which the fruit failed to develop, since the persistence of the ovary, when no seeds develop, cannot be regarded as forming a separate category as far as our present considerations are concerned. Our pedicels are classified according to the number of seeds which they produce, hence "no fruit" and "sterile fruit" both fall in the *zero* class.

The table of 4,980 entries was successfully formed and verified; that of 15,680 entries presented so many difficulties that it was finally given up in despair. Fortunately, just at the time, a relatively short process of obtaining the intra-class correlation coefficient from untabulated data was successfully worked out.

The constants published here were, therefore, obtained by two different but equally valid methods, which applied to the same material would give identical results.[19] We find for the two series:—

For fertile fruits only, $r = + .1556 \pm .0187$[20]
For sterile and fertile rays, $r = - .2149 \pm .0136$

Now these constants must be cautiously interpreted, but looking at them superficially—which is all that is possible until much more extensive and refined data are available—one is inclined to conclude *(a)* that the inflorescences vary[21] in (α) the opportunities for pollination, (β) the innate vigor (capacity for development) of the ovules, or (γ) the quantity of plastic material available for seed formation, so that when one fertile fruit has a high number of seeds, the others also tend to be high, but *(b)* that an excess of fertility in some fruits of an inflorescence is in the long run attained at the cost of the complete sterilization of others.

But these conclusions are purely tentative—chiefly useful as indicators of fertile lines of future research into a complex subject.

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19 The new method will be published shortly. The original table in the one case and the untabulated data in the other are too bulky for publication. The arithmetical routine has been carried out with exceeding care, and checked at every step.

20 I follow the general practise of taking N as the actual number of fruits in the calculation of the probable error. Possibly, we should use the number of inflorescences instead. In that case, we would have: $r = + .1556 \pm .0427$, and $r = - .2149 \pm .0384$.

21 The reader will bear in mind that these inflorescences come from a large number of plants. Hence, differences shown by inflorescences are partly, at least, the differences between individuals.

7. Correlation in Weight between the Seeds of the Fruit.

In the foregoing paragraphs, an attempt has been made to learn something of the factors influencing the number of seeds per pod. The original plan was to make these studies much wider and more detailed, and to investigate the factors influencing seed weight. The only question which can be investigated on the preliminary records is whether a difference in the capacity for seed development is to be detected in the size of the seeds from various fruits.

Of the various ways in which this problem might be approached, the most satisfactory seems to be to determine the degree of similarity in weight of seeds from the same fruit. This procedure is justified by the nature of the problem. If the *Anlagen* giving rise to some fruits are more vigorous than those giving rise to others, or the fruits better supplied with plastic materials, we might expect the seeds to be heavier, while in the less vigorous or less richly nourished fruits, they would be lighter. These factors would, to some extent, affect all of the seeds of a fruit alike, and as a result, a correlation between the weight of the seeds of the same fruit would arise. The magnitude of the intra-ovarial correlation coefficient measures (with certain restrictions)

TABLE X.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	
1	918	577	166	87	70	57	26	23	19	8	12	4	3	1	..	..	..	..	1,971
2	577	1,510	748	361	179	91	39	21	16	9	2	5	2	3	1	..	..	..	3,564
3	166	748	962	644	327	157	98	32	15	11	3	2	2	...	..	1	..	..	3,168
4	87	361	644	576	451	233	133	41	44	19	8	4	5	2	..	2	..	..	2,610
5	70	179	327	451	360	213	134	66	43	29	17	8	7	2	1	1	..	..	1,908
6	57	91	157	233	213	174	153	92	56	39	18	14	17	5	..	4	..	..	1,323
7	26	39	98	133	134	153	98	94	58	54	17	20	20	7	2	1	..	..	954
8	23	21	32	41	66	92	94	82	67	61	31	18	29	17	2	8	..	..	684
9	19	16	15	44	43	56	58	67	30	33	25	25	34	16	5	7	1	1	495
10	8	9	11	19	29	39	54	61	33	22	18	18	15	4	3	6	..	2	351
11	12	2	3	8	17	18	17	31	25	18	32	11	28	10	3	5	3	..	243
12	4	5	2	4	8	14	20	18	25	18	11	30	39	15	12	5	1	3	234
13	3	2	2	5	7	17	20	29	34	15	28	39	20	19	9	8	2	2	261
14	1	3	...	2	2	5	7	17	16	4	10	15	19	6	5	4	1	..	117
15	...	1	...	...	1	...	2	2	5	3	3	12	9	5	..	..	1	1	45
16	...	...	1	2	1	4	1	8	7	6	5	5	8	4	..	2	..	..	54
17	...	...	...	...	...	...	...	...	1	...	3	1	2	1	1	..	..	..	9
18	...	...	...	...	...	...	...	...	1	2	...	3	2	...	1	..	..	..	9
	1,971	3,564	3,168	2,610	1,908	1,323	954	684	495	351	243	234	261	117	45	54	9	9	18,000

the degree of individuality of the fruits with respect to their capacity for laying down seed-forming substance.

The 1906 series of weighings were made for this purpose. The labor involved in the preparation and verification of correlation tables with every seed used once as a first and once as a second member of an associated pair is very greatly increased by the use of varying numbers from the fruits. It is desirable, therefore, to have the same and as large a number as possible from each of the 200 fruits. Ten can easily be secured from the larger earlier maturing fruits. The fruits, therefore, are not a random sample of the whole crop, but are intentionally a selection, though only in so far as is necessary to secure those containing at least ten seeds. The seeds to be weighed were chosen quite at random by selecting those falling farthest to the right when the fruit was opened above a table.

The symmetrical intra-fruit correlation surface appears as Table X.[22] Within each fruit there are $n(n\text{-}1)$ combinations, or a total of $10 \times 9 \times 200 = 18{,}000$. The correlation coefficient is

$$r = .6759 \pm .0082$$

and the equation to the regression straight line, shown graphically in Diagram III is

$$W_2 = 1.4225 + .6759\, W_1,$$

where the constants are in the half-gram units of weighing. The close agreement of the empirical and theoretical means leaves no question concerning the linearity of regression.

The results indicate that some complex of morphogenetic and physiological factors tends very strongly to make the seeds of a fruit alike in weight. The nature of these factors and the part played by each must be determined by the application of proper biometric formulæ to more detailed records.

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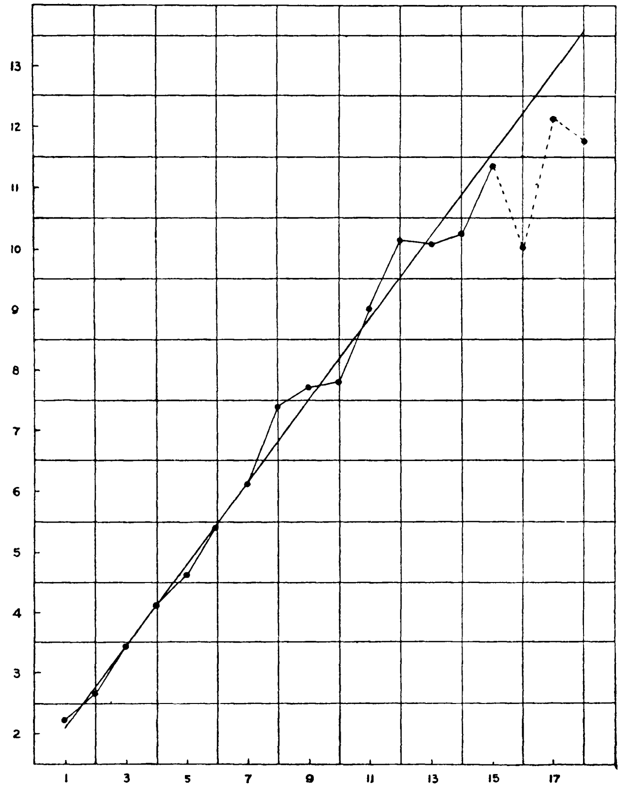
22 The seed weights are for convenience expressed in the class units given in Table VI.

DIAGRAM III.

EMPIRICAL MEANS AND FITTED REGRESSION STRAIGHT LINE, SHOWING CLOSENESS OF INTERDEPENDENCE IN WEIGHT OF SEEDS FROM THE SAME FRUIT.



IV. SUMMARY AND CONCLUSIONS.

1. The primary purpose of this paper is the recording of quantitative data on the inflorescence, fruit and seed of *Crinum longifolium* for future use in comparative studies of fertility and fecundity in plants. Such problems are immensely complex. Numerous forces are pulling, sometimes in the same, sometimes in opposite directions. Another investigator may find his material differing in some important regards from that described here, because various

conditions are different. It is, therefore, only with the explicit statement that final conclusions must await the comparative treatment of wider series of data, that I indicate some of the points of more general interest.

2. On comparative grounds, one must assume that the anomalous seed habit of *C. longifolium,* and other similar species, is not primitive but probably recently acquired from an ancestral form producing a large number of ovules per fruit. Several peculiarities of the inflorescence and fruits may be referred to the large size of the seed. We note that:—

(a) Variation in the number of flowers produced or in the number of fruits matured per inflorescence is not greater than that generally found in inflorescences. The peculiarities of the seeds apparently have not produced any effect on variation in the inflorescence.

(b) The variation in number of seeds per fruit, measured by range, standard deviation or coefficient of variation is very great. The distribution is also very skew. These conditions are probably directly due to the existence of a large number of ovules in each ovary (an ancestral characteristic?) of which only a part can, because of the great size of the seeds, be developed to maturity.

(c) The distribution of seed weight is very skew and the variability very high. This is probably to be attributed to the limitation imposed upon the tendency of a large number of ovules to develop into seeds by the inadequacy of plastic materials for all.

3. There is a moderately close positive correlation of the order $r = .35$, between the absolute numbers of flowers formed and fruits developing per inflorescence. The correlation between the number of flowers per inflorescence and the deviation of the number of fruits developing from the probable, on the assumption of proportionate fertility throughout, is negative in sign and of about the same order of magnitude. The larger inflorescences are, therefore, less

capable of maturing their ovaries into fruits than are the smaller ones.

4. There appears to be a slight negative correlation between the number of fruits per inflorescence and the number of seeds developing per fruit, *i. e.,* a decrease in the number of seeds per fruit is associated with the production of a number of fruits above the average. This result reinforces the conclusions stated under (3).

5. The intra-inflorescence correlation for number of seeds matured is positive if only fertile fruits be included, but (apparently) significantly negative, if sterile and fertile ovaries are taken at random. Apparently, therefore: *(a)* the inflorescences vary in their capacity for forming seeds, so that when one fruit is above the average in seed production, the others of the same inflorescence are also likely to be above the average in fertility; *(b)* the superior fertility (seed production) of some fruits is likely to be attained at the cost of the complete sterilization of other ovaries.

6. There is a moderately high correlation between the weight of the seeds of a fruit. There is, therefore, some complex of factors—innate vigor of ovules, availability of plastic materials, etc.,—tending to render the seeds of a fruit alike. What these factors and their intensities are, can only be ascertained by more detailed analysis of more extensive data.